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Coping styles in farmed fish: consequences for aquaculture

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Abstract

Individual differences in physiological and behavioural responses to stressors are increasingly recognised as adaptive variation and thus raw material for evolution and fish farming improvements including selective breeding. Such individual variation has been evolutionarily conserved and is present in all vertebrate taxa including fish. In farmed animals, the interest in consistent trait associations, that is coping styles, has increased dramatically over the last years because many studies have demonstrated links to performance traits, health and disease susceptibility and welfare. This study will review (i) the main behavioural, neuroendocrine, cognitive and emotional differences between reactive and proactive coping styles in farmed fish; (ii) the methodological approaches used to identify coping styles in farmed fish, including individual (group) mass-screening tests; and (iii) how knowledge on coping styles may contribute to improved sustainability of the aquaculture industry, including welfare and performance of farmed fish. Moreover, we will suggest areas for future research, where genetic basis (heritability/epigenetic) of coping styles, and the neuroendocrine mechanisms behind consistent as well as flexible behavioural patterns are pinpointed as central themes. In addition, the ontogeny of coping styles and the influence of age, social context and environmental change in coping styles will also be discussed.

Key words: behavioural syndromes, farm animals, individual variation, personality, stress response.

Introduction

In animals, including fish, individual differences in response to challenges are associated with differences in behaviour (Øverli *et al.* 2007; Réale *et al.* 2010a). Many of these associations have been shown to be consistent under stressful conditions and thus to represent coping styles in accordance with the definition by Koolhaas *et al.* (1999), as 'a coherent set of behavioural and physiological stress responses, which is consistent over time and which is characteristic to a certain group of individuals'. Terminology remains one of the main challenges when addressing the topic of consistent individual variation in physiology and behaviour. Other authors use terms such as behavioural syndromes (Sih *et al.* 2004), personality (Gosling 2001) and temperament (Francis 1990) more or less synonymously, while physiologists tend to refer to coping styles. These terms and designated definitions share common grounds such as the recognition that individual variation may be consistent and biologically meaningful, and individual differences in certain behavioural traits are consistent and predictive of other behaviours or physiological responses shown in another context. Typically, in biomedical research and agricultural sciences, the term

'coping styles' is preferred, while in behavioural ecology, the terms behavioural syndromes are more common. The range of biological parameters considered also differs between the different terms. Coping styles often include both behavioural and physiological responses to unfavourable environments and stress (Koolhaas *et al.* 1999) while behavioural syndromes include only behavioural differences and not necessarily under stress conditions. Personality and temperament, in humans, include essentially emotional reactivity traits. However, when applied to animals, the term 'personality' often ignores the emotional component. Table 1 summarises the terminology concerning individual variation. Recognising that both physiological and behavioural traits are important, throughout this review, the term 'Coping styles' will be used in accordance with the definition by Koolhaas *et al.* (1999, see above).

In fish, the importance of understanding mechanisms involved in coping styles has gained increasing attention. In particular, as conditions that are well tolerated by some individuals may be detrimental to others, the concept of coping styles is important for their welfare (Huntingford & Adams 2005; Huntingford *et al.* 2006), health and diseases resistance (Fevolden *et al.* 1992, 1993; MacKenzie *et al.* 2009; Kittilsen *et al.* 2012), performance traits (Martins 2005; Øverli *et al.* 2006a,b; Martins *et al.* 2011b) and interpretations of molecular data (MacKenzie *et al.* 2009; Johansen *et al.* 2012; Rey *et al.* 2013).

Moreover, Martins *et al.* (2011b) showed that coping styles are predictive of how stimuli are appraised, supporting the inclusion of emotional or affective states (in this case fear) as essential component of coping styles in fish. Also Millot *et al.* (2014a) shown that fish are able to retain memories of events with positive/negative valence which are retrieved by environmental cues.

Table 2 summarises the main behavioural and physiological differences between reactive and proactive

Table 1 Summary of the terminology used concerning individual variation

	Terminology	Definition	References
Individual variation and terminology			
Consistency in behaviour	Personality (temperament)	Those characteristics of individuals that describe and account for consistent patterns in feeling, thinking and behaving	Francis (1990), Gosling (2001)
Correlation between behaviours	Behavioural syndromes	A suite of correlated behaviours reflecting individual consistency in behaviour across multiple situations	Sih *et al.* (2004)
Correlation between behaviour and physiology	Stress-coping styles	A coherent set of behavioural and physiological stress responses which is consistent over time and which is characteristic of a certain group of individuals	Koolhaas *et al.* (1999)

Table 2 Behavioural and physiological differences between proactive and reactive fish

	Proactive	Reactive	References
Behavioural characteristics			
Actively escape to stressor	High	Low	Silva *et al.* (2010), Martins *et al.* (2011c), Brelin *et al.* (2005), Laursen *et al.* (2011)
Feed efficiency	High	Low	Martins *et al.* (2005a,b, 2006a,b), van de Nieuwegiessen *et al.* (2008)
Feeding motivation	High	Low	Øverli *et al.* (2007), Kristiansen and Fernö (2007)
Risk taking and exploration	High	Low	Huntingford *et al.* (2010), Øverli *et al.* (2006) , MacKenzie *et al.* (2009), Millot *et al.* (2009a)
Aggressiveness	High	Low	Øverli *et al.* (2004, 2005), Castanheira *et al.* (2013a,b)
Social influence	Low	High	Magnhagen (2007), Magnhagen and Staffan (2005), Magnhagen and Bunnefeld (2009)
Sensitive to environmental stressors	Low	High	Höglund *et al.* (2008)
Plasticity/Flexibility/Routine formation	Low	High	Chapman *et al.* (2010), Ruiz-Gomez *et al.* (2011)
Physiological characteristics			
HPI reactivity	Low	High	Castanheira *et al.* (2013a), Øverli *et al.* (2006), Trenzado *et al.* (2003)
Sympathetic reactivity	High	Low	Schjolden *et al.* (2006), Verbeek *et al.* (2008), Barreto and Volpato (2011)
Parasympathetic reactivity	Low	High	Verbeek *et al.* (2008), Barreto and Volpato (2011)
Hormonal modulation	Low	High	LeBlanc *et al.* (2012)
Oxygen consumption	High	Low	Herrera *et al.* (2014), Killen *et al.* (2011), Martins *et al.* (2011c)
Myocardial dysfunction	Low	High	Johansen *et al.* (2011)
Neural plasticity	Low	High	Johansen *et al.* (2012)
Immunity	High	Low	Kittilsen *et al.* (2012)

individuals. Nevertheless, it is imperative to note that the differentiation in coping styles may not be expressed as a binomial distribution in most of the species but rather as a continuous distribution with the majority of individuals expressing intermediate characteristics. In addition, Boersma (2011) suggested that the relative occurrence of contrasting coping styles depends on the type of population (i.e. wild or domesticated). This author showed that in wild populations of rats, the coping strategies of the individuals within a population display a binomial distribution: with extremes proactive vs. reactive individuals. Rats with an intermediate coping style are generally not present in a population in the wild because they have a lower fitness in both stable and new or instable environments. In contrast, Réale *et al.* (2007, 2010a,b) demonstrated a normal distribution of coping styles in the wild in several species. Moreover, in laboratory or domestic settings, there is less environmental pressure pushing the population into a bimodal distribution of coping styles. This means that in domesticated population a normal distribution in coping styles is usually observed (Spoolder *et al.* 1996).

Nowadays, stress-coping styles are clearly identified in fish and have contributed to the understanding of individual variation in the ability to cope with stressful events. A consensus is emerging that increased understanding of the consequences of stress-coping styles in aquaculture is important to safeguard a sustainable development of this industry.

This study will review (i) the main behavioural, neuroendocrine, cognitive and emotional differences between reactive and proactive coping styles in farmed fish; (ii) the methodological approaches used to identify coping styles in farmed fish, including individual (group) mass-screening tests; and (iii) how knowledge on coping styles may contribute to improved sustainability of the aquaculture industry, including welfare and performance of farmed fish.

Assessment of coping styles in farmed animals

Land farm animals

Assessment of coping styles in farm animals gained momentum in the late 1980s. In those studies, researchers applied the concept of coping styles to domestic livestock and started to understand how distinct individual traits were related with stress coping under common rearing conditions. For instance, in piglets, the most common test is the 'back test' (Hessing *et al.* 1993, 1994) which consists of restraining each piglet in a supine position for 1 min and classification of pigs is then based on the number of escape attempts made. Other tests commonly used in pigs and other farm animals such as cows, cattle and sheep are the open field test (Spoolder *et al.* 1996; van Reenen *et al.* 2005; Magnani *et al.* 2012), the novel object test (Spoolder *et al.* 1996; van Reenen *et al.* 2005; Magnani *et al.* 2012; Spake *et al.* 2012), the novel environment test (Hopster 1998) and the resident–intruder test (Bolhuis *et al.* 2005a; Spake *et al.* 2012). Along with behavioural responses also physiological responses are measured including cortisol responsiveness, heart rate (Korte *et al.* 1999), gastric ulceration and vocalisation (Hessing *et al.* 1993; Hopster 1998; Ruis *et al.* 2001; van Reenen *et al.* 2002; van Erp-van der Kooij *et al.* 2003; van Reenen *et al.* 2005; Spake *et al.* 2012).

Several traits attributed to proactive and reactive individuals in land farmed animals have also been identified in fish suggesting that many of such traits have been evolutionary conserved in vertebrates (see references below).

Identifying coping styles in farmed fish

Over the last years, the number of studies addressing coping styles in fish has raised rapidly. Many of these studies address farmed fish including common carp (*Cyprinus carpio*) (MacKenzie *et al.* 2009; Huntingford *et al.* 2010), Nile tilapia (Barreto & Volpato 2011; Martins *et al.* 2011b,d), Atlantic salmon (*Salmo salar*) (Kittilsen *et al.* 2009a, 2012; Vaz-Serrano *et al.* 2011), Atlantic halibut (*Hippoglossus hippoglossus*) (Kristiansen & Fernö 2007), rainbow trout (Øverli *et al.* 2005, 2006a,b; Schjolden *et al.* 2005a,b, 2006; Höglund *et al.* 2008; Ruiz-Gomez *et al.* 2008, 2011; Laursen *et al.* 2011), sea bass (Millot *et al.* 2009a,b; Ferrari *et al.* 2014) and gilthead sea bream (Castanheira *et al.* 2013a,b; Herrera *et al.* 2014) in Table 2.

Like in mammals, two main coping styles are typically recognised: proactive (active coping or bold or 'fight–flight') and reactive (passive coping or shy or 'nonaggressive').

Typically, proactive individuals are behaviourally characterised by (i) active escape from a stressor (Brelin *et al.* 2005; Silva *et al.* 2010; Laursen *et al.* 2011; Martins *et al.* 2011c); (ii) high feed efficiency (Martins *et al.* 2005a,b, 2006a,b; van de Nieuwegiessen *et al.* 2008); (iii) high feeding motivation after transfer to a new environment (Øverli *et al.* 2007) or food type (Kristiansen & Fernö 2007); (iv) high risk taking and exploratory when exposed to novelty (Øverli *et al.* 2006a; MacKenzie *et al.* 2009; Millot *et al.* 2009a; Huntingford *et al.* 2010); (v) high social rank (dominant) during aggressive encounters (Øverli *et al.* 2004, 2005; Castanheira *et al.* 2013a); (vi) low social influence (Magnhagen & Staffan 2005; Magnhagen 2007; Magnhagen & Bunnefeld 2009); (vii) low sensitive to environmental stressors (Höglund *et al.* 2008); and (viii) establishment of routines and have less behavioural flexibility (Chapman *et al.* 2010; Ruiz-Gomez *et al.* 2011) when compared to reactive individuals. Proactive individuals exhibit typical physiological and neuroendocrine characteristics such as (i) lower hypothalamus–pituitary–interrenal (HPI) activity

(Silva *et al.* 2010), as measured by basal cortisol levels; (ii) lower HPI reactivity (Trenzado *et al.* 2003; Øverli *et al.* 2007; Castanheira *et al.* 2013a), as measured by increase in cortisol over basal levels when stressed; (iii) higher sympathetic reactivity and lower parasympathetic reactivity (Schjolden *et al.* 2006; Verbeek *et al.* 2008; Barreto & Volpato 2011), measured as opercular beat rate; (iv) low hormonal modulation (LeBlanc *et al.* 2012); (v) higher oxygen consumption during stress (Killen *et al.* 2011; Martins *et al.* 2011c; Herrera *et al.* 2014); (vi) lower myocardial dysfunction (Johansen *et al.* 2011); (vii) lower neural plasticity (Johansen *et al.* 2012); and (viii) high immunity (Kittilsen *et al.* 2012) when compared to reactive individuals.

In addition to behaviour, physiological and neuroendocrine characteristics, proactive and reactive fish have also been reported to differ in cognitive and emotional traits. One of the best examples of the characterisation of coping styles in fish comes from studies using selected lines of rainbow trout (*Oncorhynchus mykiss*). These lines were segregated into high- and low-responding individuals (HR, LR) on the basis of their plasma cortisol response after confinement test (Pottinger & Carrick 1999). Studies in these lines demonstrated a link between cognition and coping styles: Moreira *et al.* (2004) showed that HR–LR individuals differed in memory retention in addition to cortisol responsiveness. The extinction of a conditioned response (i.e. how quickly the conditioned response was lost after the end of reinforcement) was greater among LR individuals.

In accordance with this, Ruiz-Gomez *et al.* (2011) showed a higher propensity to develop and follow routines (reversal learning) in LR trout. They continue to perform a learned pattern even if the conditions change. LR fish showed slower reversal learning when finding relocated feed, and it was suggested that this reflects a cognitive difference, where LR fish have a stronger tendency to develop and follow routines. This is in accordance with what have been suggested as general differences between proactive and reactive individuals, where reactive individuals react to environmental changes while proactive individuals follow predictions of the actual environment (Coppens *et al.* 2010).

Various methodologies used to characterise coping styles in fish have been adapted from those used in land farmed animals, an example is the restraining test, which is very similar to the back test commonly used in pigs. The restraining test in fish consists of holding each individual in an emerged net for a certain limited period depending on the species (Arends *et al.* 1999; Silva *et al.* 2010; Castanheira *et al.* 2013a,b). While in the net, the following behaviours have been measured: latency to escape, number of escape attempts and total time spent on escape attempts. Proactive individuals have been shown to exhibit more and longer escape attempts as compared to reactive individuals (Silva *et al.* 2010; Martins *et al.* 2011a,c). Other tests used in land farmed animals that have been adapted and applied to fish include the novel object test (Frost *et al.* 2007; Basic *et al.* 2012), the exploration test (Magnhagen & Staffan 2005; Magnhagen & Bunnefeld 2009; Chapman *et al.* 2010; Killen *et al.* 2011) and the resident–intruder test (Øverli *et al.* 2002a,b; Brelin *et al.* 2005).

Recent studies using farmed fish as models have suggested the possibility to discriminate coping styles using grouped-based test (e.g. hypoxia test developed in rainbow trout by Laursen *et al.* (2011) and adapted to gilthead sea bream by Castanheira *et al.* 2013b). Briefly, the hypoxia test consists of reducing the oxygen levels in one side of a two chambers tank and measuring the escape behaviour from the hypoxia to the normoxia side. Another group-based test is the risk-taking test (or exploration test) which consists of a tank separated in two distinct areas: safe and risk areas. Fish are placed in the safe area (darkened settling chamber), connected by a plastic tunnel or an opening to a risk area (open field). The risk area is usually associated to feed delivery zone to stimulate fish going to the nonfamiliar area (Millot *et al.* 2009b; Huntingford *et al.* 2010; Castanheira *et al.* 2013b).

Finally, it should be noted that an increasing number of studies also report that contrasting coping styles in fish are reflected in somatic and morphological traits such as developmental rate (Andersson *et al.* 2011, 2013a,b) and pigmentation patterns (Kittilsen *et al.* 2009a,b, 2012; Bäckström *et al.* 2014). Genetic markers for variable stress resistance are also increasingly explored (Rexroad *et al.* 2012). Thus, tools to characterise coping styles and personality traits in fish are becoming increasingly available which fulfils an important prerequisite for the effort towards understanding both the biological background and applied potential of this type of individual variation.

The presence of coping styles in the most important farmed fish species and the common tests used are presented in Table 3.

Consistency and plasticity of coping styles in farmed fish

One of the major gaps in the literature concerning the characterisation of coping styles in animals, including fish, is the lack of knowledge on the consistency of individual differences. This includes knowledge on both contextual consistency, that is the extent to which scores for behaviour expressed in one context are correlated across individuals with scores for behaviour expressed in one or more other contexts, when behaviour in all of the contexts is measured at the same age and time and temporal consistency, that is 'the extent to which scores for behaviour in a given context

Table 3 Summary of the evidence of coping styles in farmed fish and common tests used – freshwater fish, diadromous fish and marine fish

Fish species	Tests	Screening	Observations	References
Freshwater fish				
Common carp (*Cyprinus carpio*)	Risk taking, competitive ability	Group	Rate of exploration and competitive ability is consistent over time and related to risk-taking behaviour: individuals that explored more quickly the novel environment was the first to gain access to restricted feed	Huntingford *et al.* (2010)
	Risk taking	Group	Individual differences in behavioural responses, immune condition and baseline gene expression	MacKenzie *et al.* (2009)
Nile tilapia (*Oreochromis niloticus*)	Feed intake recovery	Individual	Individual differences in ventilation rate and correlate with the rate of feeding recovery in isolation	Barreto and Volpato (2011)
	Feed intake recovery	Individual	Proactive individuals seem to exhibit a faster recovery of feed intake after transfer into a novel environment and use feed resources more efficiently	Martins *et al.* (2011b,d)
	Feed intake recovery, novel object, restraining	Individual	Inclusion of emotional reactivity (fearfulness) and appraisal as discriminating variables between reactive and proactive individuals	Martins *et al.* (2011a)
African catfish (*Clarias gariepinus*)	Feed intake recovery, feeding behaviour	Individual + Group	Proactive individuals seem to exhibit a faster recovery of feed intake after transfer into a novel environment and use feed resources more efficiently. Feeding behaviour could be used as a predictor of feed efficiency	Martins *et al.* (2005a,b, 2006a,b,c)
	Feed intake, aggression	Individual + Pairwise	Individual differences in residual feed intake are related with differences in aggressive behaviour: more efficient individuals are more aggressive	Martins *et al.* (2008)
	Alarm cues, feeding behaviour	Individual	Feeding efficiency (residual feed intake) related with opposite behavioural responses to conspecific skin extract	van de Nieuwegiessen *et al.* (2008)
	Escape test	Individual + Group	Behavioural responses to the escape test (after a group-housed period) changed according to the group composition	van de Nieuwegiessen *et al.* (2010)
Perch (*Perca fluviatilis*)	Habitat utilisation and feeding activity in visual contact with a potential predator, Risk taking	Individual + Group	Proactive individuals spent more time in the open field and tended to be faster to enter in unknown environments. Modulation of individual behaviours by other group members	Magnhagen and Staffan (2005), Magnhagen (2007), Magnhagen and Bunnefeld (2009)
Diadromous fish				
Atlantic salmon (*Salmo salar*)	High/Low stress response	–	Individual differences in disease resistance in lines selected for high and low post-stress plasma cortisol levels	Fevolden *et al.* (1993)
	Feeding in isolation, confinement	Individual	HR (more reactive) fish showed increased susceptibility to infectious. Pigmentation profiles are correlated with stress cortisol response. Distinct vulnerability to parasites correlates with pigmentation (high/low black skin spots)	Kittilsen *et al.* (2009a,b)
	Resume feeding in isolation	Individual	Early emerging individuals showed a shorter time to resume feeding after transfer to rearing in isolation	Vaz-Serrano *et al.* (2011)
	Aggression	Pairwise		

Table 3 (Continued)

Fish species	Tests	Screening	Observations	References
Rainbow trout (*Oncorhynchus mykiss*)			Lower brain serotonergic activity in socially naïve fry with big yolk and higher propensity for social dominance and aggression	Andersson and Höglund (2012)
	Emergence from spawning gravel	Group	Relationship between characteristics expressed in early development and stress-coping styles. The LR fish line has bigger eggs, yolk reserves and faster developmental rate	Andersson *et al.* (2013a,b)
	Novel object, resident –intruder, confinement	Individual	Individual differences were behavioural constant, but no differences were found between LR and HR lines	Basic *et al.* (2012)
	Confinement	Group	Inflammatory challenge with bacterial pathogens reported distinct disease resistance between coping styles	Fevolden *et al.* (1992)
	Novel object	Individual	Social context is an important modulator of coping styles. Bold fish may be more flexible to changing conditions as opposed to shy individuals	Frost *et al.* (2007)
	Initiation of avoidance swimming (larvae)	Individual	Yolk sac fry originating from the HR strain were more sensitive to environmental stressors and have shown a shorter reaction time to low oxygen levels	Höglund *et al.* (2008)
	Confinement	Individual	HR fish seem to be associated with cardiac remodeling and altered gene expression	Johansen *et al.* (2011)
	Confinement, social stress (dominant resident fish)	Individual + Group	Neurobiological mechanism underpinning differences in plasticity associated with distinct coping styles	Johansen *et al.* (2012)
	Confinement	Individual	Differences between the HR and LR fish strain in the degree of pigmentation	Kittilsen *et al.* (2009b)
	Hypoxia	Group	Behavioural responses to hypoxia can be used as a noninvasive method for sorting fish according to stress-coping styles	Laursen *et al.* (2011)
	Confinement, heat shock, feed intake recovery	Individual	HR fish has a general response to environmental changes reflected in their greater and faster heat shock response and lower oxidative protein damage in response to high temperatures	LeBlanc *et al.* (2012)
	Exploratory behaviour, Risk taking	Individual + Group	The importance of the genetic regulation: isogenic lines with contrasted behavioural responses to a set of environmental stimuli	Millot *et al.* (2014b)
	Emersion, confinement	Group	HR–LR individuals differed in memory retention	Moreira *et al.* (2004)
	Locomotor activity, smaller conspecific intruder, feed intake	Individual + Pairwise	Behavioural and physiological differences between HR and LR fish established differences in performance	Øverli *et al.* (2002)
	Aggressive behaviour, feed intake, confinement	Individual + Pairwise	LR fish were more aggressive when placed in a dominant social position	Øverli *et al.* (2004a)
	Confinement, locomotor activity, feed intake	Individual	Individual differences in behavioural responses. Synthesis and metabolism of monoamine neurotransmitters and their metabolites were elevated after stress to a larger degree in HR fish	Øverli *et al.* (2004b)

Table 3 (Continued)

Fish species	Tests	Screening	Observations	References
	Feed intake recovery, confinement	Individual	Behavioural indicators of stress-coping styles related with sex difference. Immature men resumed feeding after transfer to social isolation quicker than men. Women settling down and ceasing to move in a panic-like manner quicker than men during the confinement	Øverli *et al.* (2006a)
	Crowded/uncrowded conditions	Group	Distinct susceptibility under crowded condition and more feed waste in units containing HR when transported	Øverli *et al.* (2006b)
	Feeding behaviour	Individual	Differences in responsiveness to environmental change: LR fish shown to develop routines more easily	Ruiz-Gomez *et al.* (2011)
	Feed intake recovery, conspecific intruder	Individual + Pairwise	Behavioural plasticity is limited by genetic factors determining social position in early life. Some behavioural differences can be modified by experience	Ruiz-Gomez *et al.* (2008)
	Confinement	Group	Differences between the HR and LR fish in plasma amino acids and liver glycogen concentration	Trenzado *et al.* (2003)
	Crowded/uncrowded conditions	Group	Performance discrepancy between the HR and LR fish related with competitiveness/aggressiveness. Differences in plasma glucose levels and glycogen levels	Trenzado *et al.* (2006)
Brown Trout (*Salmo trutta*)	Feed intake recovery, resident–intruder, hypoxia, confinement	Individual	Individual differences in behavioural responses on resident–intruder, hypoxia and confinement. No differences in feed intake recovery	Brelin *et al.* (2005)
Marine fish				
Gilthead Sea bream (*Sparus aurata*)	Restraining, aggression	Individual + Pairwise	Fish with lower cortisol levels (proactive) when exposed to stress are more aggressive	Castanheira *et al.* (2013b)
	Feed intake recovery, novel object, restraining, risk taking	Individual + Group	Behavioural differences are consistent over time and predictable based on other behaviours. Possibility to predict behaviour in groups from individual personality traits	Castanheira *et al.* (2013a)
	Risk taking, hypoxia	Individual + Group	Risk-avoiders (reactive) behaviours were negatively correlated to movement and oxygen consumption rates in metabolic chambers	Herrera *et al.* (2014)
Sea bass (*Dicentrarchus labrax*)	Feed intake recovery, exploration, restraining, risk taking, hypoxia	Individual + Group	Behavioural differences were not consistent over time or across context in individual-based tests. In contrast, strong individual consistency was observed for all variables measured in group-based tests. Hypoxia-avoiders had lower cortisol rate and higher activity and were higher risk takers: the 3 characteristics of proactive coping style	Ferrari *et al.* (2014)
	Exploration + swimming activities after a stimulation	Individual	Whatever the level of domestication and selection for growth fish presented the	Millot *et al.* (2009a)

Table 3 (Continued)

Fish species	Tests	Screening	Observations	References
			same flight response and stimulus exposure induced a significant decrease in exploratory behaviour and swimming activity. Only one generation of captivity could be sufficient to obtain fish presenting the same coping style characteristics (bolder) than fish reared for at least two generations	
	Risk taking	Group	Wild fish were generally bolder than selected fish during two-first days of test but showed a decrease in risk-taking behaviour during a third-day test. Selected fish showed a constant increase in their risk-taking behaviour over time	Millot *et al.* (2009b)
Senegalese sole (*Solea senegalensis*)	Feed intake recovery, restraining	Individual	Proactive fish exhibit shorter feeding latency, higher duration of escape attempts and lower undisturbed cortisol levels than passive individuals	Silva *et al.* (2010)
	Restraining	Individual	Individual differences in metabolism are predictive of distinct coping styles	Martins *et al.* (2011a)
Sole (*Solea solea*)	Novel environment, light avoidance, feeding efficiency	Group + Individual	Proactive fish (high swimming activity) were most feed efficient and grew faster	Mas-Muñoz *et al.* (2011)
Halibut (*Hippoglossus hippoglossus*)	Swimming behaviour, feed intake	Group	Reactive individuals were unable to adapt, or adapted very slowly, to floating feed showed decreased feed intake and increased stereotypic (surface swimming) activity – reflects high routine formation	Kristiansen and Fernö (2007)

at a given time are correlated across individuals with scores for the same behaviour in the same context at a later time' (Stamps & Groothuis 2010).

Studies in the HR/LR rainbow trout lines showed that proactive and reactive individuals exhibit consistent traits. Over a period of 7 days, feeding responses after transfer into a novel environment, responses to a novel object, aggressiveness and responses to confinement were behaviourally constant, but no differences between lines were apparent (Basic *et al.* 2012). The ontogenic consistency of these traits was also demonstrated by Höglund *et al.* (2008) and Andersson *et al.* (2011, 2013a,b).

However, most of the studies on coping styles characterisation have been performed on selected HR–LR fish lines (Øverli *et al.* 2005, 2007) which raises the question whether similar consistency responses can be observed in nonselected populations. In line with the previous information, recent studies on nonselected populations seem to support the consistency of behavioural responses both over time and across context. Castanheira *et al.* (2013b) using a nonselected population of gilthead sea bream (*Sparus aurata*) showed that individual differences in risk-taking behaviour and escaping behaviour in response to stressors are consistent over a period of 15 days. Moreover, the same authors also showed that some behaviour can be used to predict other behaviours expressed in a different context (e.g. individuals that took longer to recover feed intake after transfer into a novel environment, exhibited higher escape attempts during a restraining test and escaped faster from hypoxia conditions). Similar results, consistency in

behaviour response to changes in their environment over time and across situations, were obtained in nonselected rainbow trout juvenile by Schjolden *et al.* (2006). Contrasting results were obtained in European sea bass where no over time and across-context consistency was observed in individual-based tests, whereas group-based tests results (risk-taking and hypoxia tests) were consistent over time (Ferrari *et al.* 2014).

Consistency of individual differences is a key element to identify coping styles in fish. However, this does not exclude the possibility that individuals change their coping style over time and context. In fact individual plasticity, that is the extent to which the behaviour expressed by individuals with a given genotype in a given context at a given age and time varies as a function of the set of conditions experienced by those individuals before the behaviour was expressed (Stamps & Groothuis 2010), is very important because it allows individuals to adjust their behaviour to novel or instable environments. Few studies have addressed how plastic, proactive and reactive coping styles are. Frost *et al.* (2007) suggested that social context is an important modulator of coping styles in rainbow trout. These authors showed that bold individuals observing another's losing fights or with lower responses to novelty (novel objects and novel prey) reduced their boldness. However, shy individuals just alter their behaviour (increase their boldness responsiveness) when their relative competitive ability was similar or higher than their conspecifics. These results suggest that bold individuals may be more flexible to changing conditions as opposed to shy individuals (Frost *et al.* 2007). Similar differences in behavioural plasticity have been documented during feeding response in presence of the novel object. Basic *et al.* (2012) showed that proactive individuals adopt a more flexible behaviour by suppressing feed intake in presence of the novel object. In contrast, Ruiz-Gomez *et al.* (2011) have reported opposite results, that is LR (proactive) individuals seem to be more fixed in responses (relocated feed) when confronted with a new situation in contrast with HR individuals.

Individuals differ in how the environmental stimuli are appraised and how they are able to adjust and adapt their physiology and behaviour to help them cope more effectively. Part of this plasticity is supported and influenced by cognition and neural plasticity. The underlying neurobiological mechanism underpinning differences in plasticity between reactive and proactive individuals have been recently studied by Johansen *et al.* (2012) in the HR/LR rainbow trout lines. These authors measured genes involved in neural plasticity and neurogenesis (PCNA, BDNF, NeuroD and DCX) using quantitative PCR in brains of rainbow trout under baseline conditions and in response to short-term confinement and long-term social stress. They showed that a higher degree of neural plasticity in reactive individuals might provide the ideal conditions to support their higher behavioural flexibility as opposed to proactive individuals.

Furthermore, Ebbesson and Braithwaite (2012) reviewed the influence of neural plasticity and cognition shaped by the environmental experiences in several fish species. These authors agree that neural plasticity aids in the adaptation and flexibility, demanding by the diverse environments in which fishes live. These make the brain more sensitive to the surrounding environment moulding the adaptive responses to the environment both over the individual life and over evolutionary time.

However, there is still a long way to go in understanding plasticity of coping styles in order to improve the management and welfare of aquaculture populations.

Aspects of how coping styles change with age, social context and new environmental conditions should be explored in the future. Environmental changes might be particularly relevant during this era of an ongoing global climate change. Global warming could cause changes in species behaviour and life history (Kling *et al.* 2003). The impacts of climate change in aquaculture can be direct, for example changes in water temperature, or indirect such as the increase of fishmeal costs and its consequences for aquaculture feeds. The recent approach by Dingemanse *et al.* (2009) offers a theoretical framework to help understanding plasticity of coping styles. They proposed the concept of behavioural reaction norms, that is measuring individual behavioural response over an environmental gradient (e.g. social environment, environmental changes). According to the same authors, the same behaviour can be measured over multiple environmental gradients and individual behaviour can be described as a linear regression line linking the response with the environmental conditions. In the linear regression, the intercept of the line describes the average individual level of the behaviour and the slope represents the individual degree of plasticity.

Using temperature as an environmental gradient, on a recent work with zebrafish, Sonia Rey *et al.* (in press, 2015) showed differences in thermal preferences for proactive and reactive fish under a thermal gradient. Proactive individuals preferred higher temperatures than reactive reflecting differences already detected on basal metabolic rates and different acclimation and environmental adaptation capacities between both coping styles.

Proxies for measuring coping styles in fish

Coping styles characterisation in fish can be time consuming, especially when individual-based tests are used. Therefore, several proxies have been suggested in the literature to characterise coping styles without the need to undertake complex behavioural tests.

Ventilation rate has been shown to be a sensitive indicator of fish physiological responses to stress. Barreto and Volpato (2011) observed that ventilation rates of Nile tilapia were correlated with the feeding resumption in isolation. Individuals with high ventilation rates resumed feeding later than fish with low ventilation rates.

Skin pigmentation has also been suggested to predict coping styles in fish (Kittilsen *et al.* 2009a,b, 2012). High spotted salmonids showed lower cortisol levels than lower spotted conspecifics (Fig. 1). Visual markers provide a suitable tool that can be easily combined with other common procedures, such as size-grading or vaccination. Furthermore, Kittilsen *et al.* (2012) provided evidence for individual variation in parasites incidences while screening distinct coping styles. Individuals with high incidence of black skin spots harboured fewer ectoparasites (sea lice) as compared to less pigmented fish.

Observations of ear and tail postures are reliable noninvasive method for assessing emotional reactivity in pigs (Reimert *et al.* 2013) and sheep (Reefmann *et al.* 2009) and have been suggested as proxies for coping styles screening. In fish, very little is known about the link between body postures and coping styles. Recently, Martins *et al.* (2012) used fin spreads (defined as a sudden elevation of the dorsal fin) to distinguish bold and shy individuals of the colonial fish, *Neolamprologus caudopunctatus*. Results showed that reactive individuals exhibited a higher number of fin spreads in response to novelty.

The time to reach the first feeding in salmonids has also been suggested to predict coping styles. Recently, Andersson *et al.* (2013b) reported a coupling between stress-coping styles and the time to reach first feeding (low cortisol responders had larger yolk reserves at emergence time) which can be used as a proxy.

What are the consequences of different stress-coping styles in farmed fish for aquaculture?

The presence of coping styles is now well recognised in farmed fish, and its implication for aquaculture can be widespread. Individual fish within a population often differ in how strongly they respond, behaviourally and physiologically, under stress conditions. A failure to accommodate the coping styles of fish under farming conditions can lead to problems linked with production (e.g. aggression, growth and disease resistance).

Growth performance and energetics

One of the best examples of the implications of coping styles in performance traits comes from studies with African catfish (Martins 2005). By studying individual differences in growth and how these relate with individual differences in feed intake, feeding behaviour and feed efficiency, Martins (2005) showed that the most efficient individuals were those reacting quicker to the presence of pellets and consuming their meals faster after transfer into a novel environment. These individuals were also those that exhibited a lower cortisol response after acute stress. All these characteristics (better feed efficiency and lower stress responsiveness) are clearly beneficial under aquaculture conditions.

Several studies revealed that coping styles play an important role in growth performance and feed conversion. In common carp, the competitive ability (success in gaining access to a spatially restricted feed source) was shown to be consistent over time and related to risk-taking behaviour (Huntingford *et al.* 2010). The same behavioural characteristics have been observed on sea bass (Millot *et al.* 2009b). Data from Martins *et al.* (2011a,b,d) have shown that proactive individuals (*Nile tilapia*) seem to exhibit a faster recovery of feed intake after transfer and to use feed resources more efficiently. In Atlantic salmon conditions that normally prevail in intensive rearing systems (e.g. restricted feeding regimes, high density) may favour proactive individuals (Huntingford 2004; Huntingford & Adams 2005).

Coping styles have also been linked with differences in metabolism (Huntingford *et al.* 2010; Martins *et al.* 2011c). In nature, the metabolic rate of an animal is linked

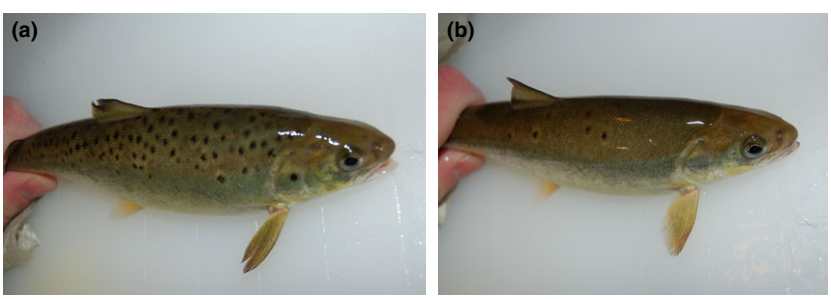

Figure 1 Distinct pigmentation profiles in Atlantic salmon defined as (a) 'spotted', that is, stress resistant and proactive and (b) 'non-spotted', that is, stress sensitive and reactive. Reproduced with permission from Kittilsen *et al.* (2009b).

to the willingness of risk taking while foraging (Careau *et al.* 2008). Hence, increased energetic requirements in individuals with a higher metabolic demand could require them to forage more often or take more risks to achieve a higher rate of feed intake (Abrahams & Sutterlin 1999; Finstad *et al.* 2007). Huntingford *et al.* (2010) and Herrera *et al.* (2014) reported that in carp and sea bream, respectively, the risk-taking behavioural phenotype is associated with a relatively high metabolic rate, while the risk-avoiding phenotype is associated with a lower rate. Killen *et al.* (2011) reported in sea bass that the amount of risk taking among individuals was positively correlated with their routine metabolic rate. However, Martins *et al.* (2011c) have reported opposite results in metabolic rate (oxygen consumption) measured when Senegalese sole were housed in respirometry chambers. These authors suggested that different individuals reacted differently when housed in the metabolic chambers that functioned as confinement chambers. Individuals that consumed less oxygen in a respirometry chamber were also the individuals that reacted sooner to a confinement stress (typical from proactive coppers). This apparent contradiction may have to do with the passive benthic life-style sole, compared to other more active fish species.

In addition, yolk sac fry originating from the HR strain were more sensitive to environmental stressors and have shown a shorter reaction time to low oxygen levels (Höglund *et al.* 2008). This suggests that differences in coping styles are expressed at early developmental stages before social or environmental interference. Proactive individuals seem to have a 'fast' development strategy (or fast pace of life) as demonstrated by an earlier hatching and consumption of egg yolk reserves as compared to reactive (Andersson & Höglund 2012). Such life strategy has an impact on metabolic needs and most likely on the nutritional requirements. For instance, optimal dietary lipid content could depend on coping styles because metabolic rates are different and hence energy requirements could vary.

In rats, metabolic differences between coping styles have been associated with metabolic diseases (Boersma 2011). Using selected Roman low-avoidance (RLA) and Roman high-avoidance (RHA) rats, Boersma (2011) showed that different strains differ in plasma insulin levels, both in baseline conditions and during the intravenous glucose tolerance tests. Reactive RLA individuals were associated with insulin resistance and elevated levels of plasma leptin, free fatty acids levels, liver triglycerides and an increased visceral fat content, especially when over feeding a high fat diet. Proactive RHA individuals were extremely resistant to diet-induced insulin resistance. Thus, coping styles of an individual seem to be associated with particular metabolic and (patho-)physiological characteristics.

Selection programmes

Selection programmes in farmed fish focus essentially on growth performance (Gjedrem 2005). As shown by Martins *et al.* (2005c), individuals exhibiting fast growth are often included in a proactive coping style. However, proactive individuals have also been shown to be more aggressive (Øverli *et al.* 2004; Castanheira *et al.* 2013a). Selection for fast growing individuals may result in co-selection of undesirable traits such as aggression. Aggressiveness has been linked with a diversity of aquaculture problems including decreased feed intake, growth dispersion, chronic stress and disease vulnerability (Ashley 2007). Furthermore, fighting brings a significant cost in terms of increased energy expenditure that may promote inefficient growth. In addition, aggression among fish in production systems can be a cause of skin and fin damage. This damage can directly reduce the value of the farmed product and increase the vulnerability to diseases. Moreover, proactive individuals have also been shown to develop routines more easily (Frost *et al.* 2007; Ruiz-Gomez *et al.* 2008, 2011; Basic *et al.* 2012). Such characteristic may be more advantageous under stable conditions provided by intensive husbandry systems but prejudicial in extensive or semi-intensive husbandry systems with lower standardised conditions.

Disease resistance and parasites

Another important implication of coping styles in farmed fish is the different disease susceptibility exhibited by proactive and reactive individuals. Diseases are one of the main challenges in aquaculture and can represent a considerable financial burden to the farmer. Studies on inflammatory challenge with bacterial pathogens reported distinct disease resistance between coping styles (Fevolden *et al.* 1992, 1993; MacKenzie *et al.* 2009).

Fevolden *et al.* (1993) suggested selection targeting distinct coping styles rather than for specific immune traits, selecting for a broad spectrum of defence mechanisms and hence affecting resistance to several diseases.

Moreover, MacKenzie *et al.* (2009) showed distinct regulation of proinflammatory gene expression suggesting that fundamental differences in cytokine regulation exist in fish with distinct coping styles. In particular, tumour necrosis factor-alpha (TNF-α) and interleukin 1-beta (IL1-β), putative cytokines involved in the development of inflammation in fish, differed between proactive and reactive individuals.

Among the diseases, salmon lice are considered a major threat to marine salmonids farming (Johnson *et al.* 2004) the evidence that salmon with higher black skin spots harboured fewer mature female lice carrying egg sacs suggests that individual host traits may decrease parasite infestation.

Moreover, Øverli *et al.* (2014) demonstrate that the presence of sea lice affects behaviour and brain serotonergic activity in Atlantic salmon. Still, further studies should address the biology behind coping styles and resistance to parasites, bacteria and viruses.

Furthermore, Kittilsen *et al.* (2009b) established that distinct pigmentation profiles are correlated with stress cortisol response in salmonids (Fig. 1). Low cortisol responders were found to be consistently more spotted than high cortisol responders. Another study by the same authors, Kittilsen *et al.* (2012) provided evidence for individual variation in parasites resistance to sea lice, particularly salmon louse (*Lapeophtheiras salmonis*) carrying egg sacs.

Fish welfare

In most fish species, chronic or acute stress is considered as the main factor reducing animal welfare in intensive husbandry productions (Huntingford *et al.* 2006; Ashley 2007). However, despite the link between acute response to challenges and coping styles, very little information is available about chronic stressors and coping styles.

One of the best examples used to discriminate distinct susceptibility to chronic stressors was performed using selected lines of wild house mice. Strains of mice have been created through selective breeding for divergent hypothalamic–pituitary–adrenal axis responses to a standardised aggressiveness test: Short Attack Latency (SAL), high aggressive/proactive, and Long Attack Latency (LAL), low to nonaggressive/reactive (Benus *et al.* 1991). Using these lines, Veenema *et al.* (2003) showed that response to a chronic stressor resulted in symptoms in LAL (proactive) mice characterised by decreased body weight, elevated plasma adrenocorticotropic hormone (ACTH) and corticosterone levels and a lower hippocampal mineralocorticoid receptor (MR): glucocorticoid receptor (GR) ratio.

Korte *et al.* (2005) mention that adaptive processes, actively maintain stability through change (allostasis), are dependent on the personality type and associated stress responses. The benefits of allostasis and the costs of adaptation (allostatic load) lead to different trade-off in health- and stress-related diseases, reinforcing that both coping styles (proactive/reactive) can be successful under different environmental conditions.

Furthermore, van de Nieuwegiessen *et al.* (2010) showed that chronic stressors (stocking density) affect the performance traits in African catfish differently according to coping strategies. Fish housed at high density showed an increase in activity and decrease in aggression levels. In addition, at high density, reactive individuals reared in mixed groups showed a comparable growth rate to intermediate and proactive individuals. It seems that the presence of intermediate and proactive individuals stimulates the feeding motivation of reactive individuals.

Undoubtedly, coping styles play an important role in how different individuals appraise the housing environment and thereby their welfare status. Huntingford and Adams (2005) reviewed the welfare consequences of coping strategies in salmonids. They suggest that when fish are housed at high densities and with a predictable feed source, as is usually the case in intensive husbandry systems, reactive individuals may fail to flourish. Another interesting question related with high densities is the difference on how proactive and reactive individuals react to the suppression of aggressive behaviour induced by crowding, that is the propensity for higher aggression in proactive individuals suggests that they will suffer most in high densities.

In contrast to Huntingford and Adams (2005), no indications were found for welfare consequences of different coping strategies in intensive husbandry systems in African catfish (van de Nieuwegiessen *et al.* 2010). Although an impaired growth performance of reactive fish housed in reactive groups was shown, no effects were detected in reactive fish housed in mixed groups, which is the common rearing practice.

Based on these results, individual coping styles should not be used as a welfare indicator, but one may infer a welfare problem when the behaviour identified under the proactive/reactive continuum changes. Even though the housing environments may have profound effects on behaviour and welfare. For example, in pigs, the environmental enrichment effects were shown to be much higher in LR than in HR and were reflected in more time on play behaviour and more oral manipulation of pen mates (Bolhuis *et al.* 2005b). In addition, the same authors showed that the effect of environmental enrichment on weight gain may differ for pigs with divergent coping styles. In fish, the effect of environmental enrichment (i.e. substrate availability) as behavioural and physiological indicators of welfare was study by Galhardo *et al.* (2008) whom showed that the absence of substrate decreased territorial behaviour, increase aggression levels, cortisol and glucose; all of which are suggestive of a stress-related context. This suggests that the welfare of at least some fish species may be negatively affected by the absence of substrate or other environmental enrichment, and this effect may change in distinct fish coping styles.

Furthermore, aggressiveness level is one of the differences between proactive and reactive individuals. Literature suggests that proactive individuals show high levels of aggressiveness (Øverli *et al.* 2004 Castanheira *et al.* 2013b). Aggression has been linked with a diversity of aquaculture-relevant problems including decreased feed intake, growth dispersion, chronic stress and disease vulnerability (Hun-

tingford & Adams 2005; Martins *et al.* 2011e) which as a consequence can impair fish welfare.

Moreover, Vindas *et al.* (2012, 2014) showed good evidence that Atlantic salmon possess a nervous system and a brain sufficiently complex to demonstrate individual responses to frustrations conditions when an omission of an expected reward occurs. Deviation from routine feeding practices, in intensive farming conditions, could have negative consequences, in terms of both production and welfare as a consequence of frustration-induced agonistic behaviours.

Knowing that farmed fish have coping styles and that coping styles differ in how they appraise their environment may help designing farming environments that are more diverse and could improve the welfare of individuals with different coping styles. In turn, this may increase production output.

Flesh quality

Nowadays, there is evidence showing that inadequate fish husbandry results in lower meat quality (Robb *et al.* 2000; Ribas *et al.* 2007; Matos *et al.* 2010, 2011). Studies show that fish subjected to stress prior to and during slaughter, in particular salmonids, display a softer texture and lower flesh quality (Kiessling *et al.* 2004; Bahuaud *et al.* 2010). Some studies suggest that the production of low cortisol-responsive fish could benefit commercial parameters such as flesh quality (Pottinger 2001). High fillet quality (e.g. textural characteristics, freshness and health value) is a requirement for feed production, and coping styles can attenuate or aggravate the effect of stressors on filet quality. However, knowledge on the mechanisms responsible for individual differences in flesh quality is still largely unknown.

Production systems

It is also important to understand how divergent coping styles perform in different aquaculture production systems. Recirculating aquaculture systems (RAS), for example, are expected to expand in the future as they offer the possibility to have a high production with a minimum ecological impact (Martins *et al.* 2010).

Mota *et al.* (2014) showed that steroids (glucocorticoids, androgens and a progestin) in their free and conjugated forms tend to accumulate in the rearing water of commercial RAS at levels that can potentially be detected by some fish species. However, we still do not know how sensitive the different coping styles are to the re-uptake of steroids and olfactory cues present in the water and how such sensitivity can induce different welfare levels.

Furthermore, the range of the coping styled spectrum that leads to maximum growth performance, highest welfare condition and disease resistance, may change depending on the husbandry system, once different types of intensive, semi-intensive or extensive systems present very different social and environmental conditions to fish.

Future perspectives

Coping styles are present in a variety of farmed fish and may impact aquaculture in different ways. However, one of the main difficulties in understanding the implications of coping styles under farming conditions is the methodology available that relies heavily on individually based tests. Screening in isolation may induce significant stress in social species. Consequently, the development of grouped-based tests (Fig. 2) may in the future facilitate mass screening of fish stocked at high densities and therefore may be more easily applied under farming conditions. Examples of

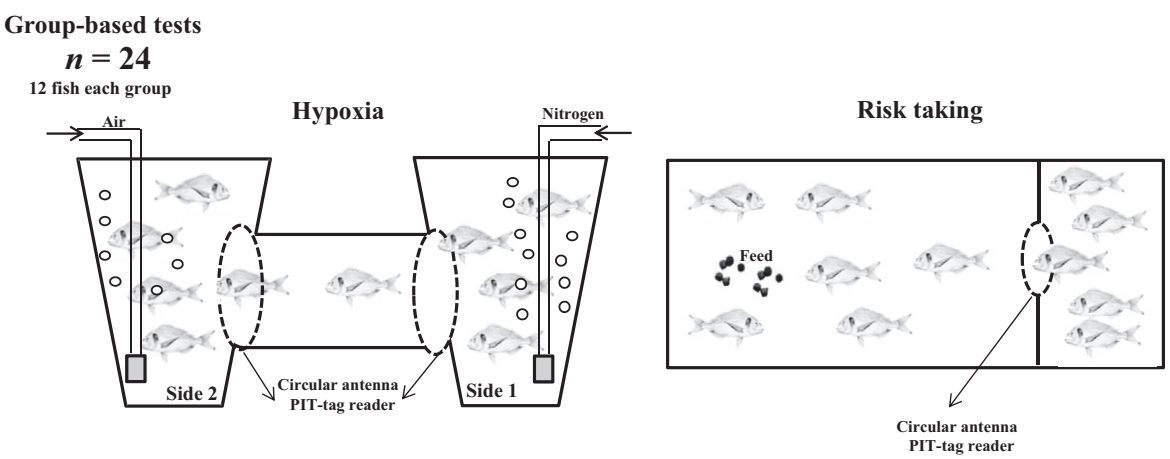

Figure 2 Schematic representation of the group-based tests used to determine coping styles in Gilthead seabream *Sparus aurata*. Reproduced with permission from Castanheira *et al.* (2013b).

potential mass-screening tests are the hypoxia and the risk-taking tests (Millot *et al.* 2009b; Huntingford *et al.* 2010; Laursen *et al.* 2011; Castanheira *et al.* 2013b; Ferrari *et al.* 2014). Additionally, further studies should be considered to validate the temporal consistency over time of the distinct traits. One of the limitations of the available knowledge regarding the temporal consistency is that it refers always to short-term consistency (usually a few weeks) (Basic *et al.* 2012; Castanheira *et al.* 2013b). However, van Reenen (2012) demonstrated long-term consistency of individual differences in behavioural and adrenocortical responses of dairy cattle to acute stressors. The observations were recorded in rearing period (6–7 months), gestation (22–24 months) and first lactation (25–29 months). They showed that individual differences in struggling in a restraint test at 7 months of age predicted those in open field locomotion during first pregnancy. In addition, individuals with high cortisol responses and reactive behaviour measured as high avoidance and less exploration to open field and novel object tests at 6 months of age, also exhibited high cortisol responses to both tests at 29 months of age. Similar studies over longer periods of time should be undertaken also in fish.

Measures of HPA axis reactivity, locomotion, vocalisation and adrenocortical and behavioural responses to novelty contributed to the understanding of ability to cope with stress and supporting the idea that stress responsiveness may be mediated by multiple independent underlying traits. Some authors have suggested that cortisol and behavioural responses to stressors are linked to two independent dimensions of stable trait characteristics (Koolhaas *et al.* 2010). These authors suggested that the quality of the response to a challenging condition (coping style) is independent from the quantity of that response (stress reactivity). According to the same authors, the physiological responses to stress such as the HPI axis reactivity (one of the most significant differences between proactive and reactive individuals) are more related to an emotional response to stress than to coping styles. Eventually, a decoupling of these axis, coping styles and emotional, could bring new light to understand the pronounced individual variation in plasma cortisol response observed. It is also important to perform studies regarding the influence of age, environmental conditions, nutrition and social group in coping styles. In other comparative models (e.g. cows, pigs), coping styles can change partly according to the social environment (van Erp-van der Kooij *et al.* 2003; van Reenen 2012). In addition, van Erp-van der Kooij *et al.* (2003) showed that coping styles in piglets can change according to the social environment although at an older age, this ability was lost.

In addition, different coping styles also differ in their adaptability towards shifts in environmental conditions. In mice, Benus *et al.* (1988) showed that individual differences in aggressiveness (a component trait of coping styles) explain differences in adaptation to external factors. The adaptation to a new photoperiod cycle took twofold long in the aggressive mice. However, in farmed fish, there are no similar studies in literature.

Still, studies in farmed fish such as the selected trout lines can open the possibility to use fish as simpler models to understand underlying mechanism of coping styles in vertebrates such as those related to neural activity and their implications in behaviour.

The knowledge of coping styles can help to improve the sustainability of production through the establishment of more fine-tuned culture strategies. In this way, the feed waste can be minimised as each coping style is related to particular physiological and behavioural responses and some culture variables could be adjusted. Moreover, the genetic basis (heritability/epigenetics) of coping styles, disease susceptibility as well the neuroendocrine mechanisms behind consistent as well as flexible behavioural patterns are here pinpointed as central themes and open research lines on application of coping styles to aquaculture.

Conclusions

The presence of coping styles is now well recognised in farmed fish, and its implication for aquaculture can be wide as here reviewed. Taken together, the fairly extensive literature on coping styles in fish shows that screening for coping styles is species specific. The recent development of group-based tests and the use of proxies may provide an opportunity for mass screening in the future. Mass screening into different coping styles may help optimising the production systems as optimal conditions for proactive individuals are likely to be different from those of reactive individuals.

In addition, the recognition that farmed fish exhibit coping styles means that a number of behavioural and physiological responses will vary as part of a common 'package' that should be taken into consideration when designing selection programmes.

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Competing interests

The authors have declared that no competing interests exist.

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